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THE DISTRIBUTIONS OF THE GLADIATOR FROGS (*HYLA BOANS* GROUP) IN COLOMBIA, WITH COMMENTS ON SIZE VARIATION AND SYMPATRY

John D. Lynch
Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia. jlynch@ciencias.unal.edu.co

Ángela M. Suárez-Mayorga
Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia. asuarez@ciencias.unal.edu.co

ABSTRACT

Five species of gladiator frogs (the *Hyla boans* group) occur in Colombia. *Hyla wavrini* barely enters Colombia (it is confined to the extreme eastern edge of the country) and *H. rosenbergi* is endemic to the biogeographic Chocó. The other three species are more widely distributed. *Hyla boans* is found in the Chocó, Middle Magdalena, and Amazonas-Orinoquia below 1000 m. *"Hyla crepitans"* is found in the Magdalena drainage as well as the western edge of the Orinoquia and less commonly along the Caribbean coast and in the Maracaibo Basin. This species occurs from sea level to more than 2000 m. *Hyla pugnax* occurs across the Caribbean lowlands and up the Magdalena valley as well as in the Maracaibo Basin and at a few cis-Andean sites, but always below 500 m. Sympatry is relatively common between *H. boans* and *H. rosenbergi* but, less common between *H. boans* and either *"H. crepitans"* or *H. pugnax*. Maximal sympatry results in sympatry of *H. boans, H. pugnax,* and *H. rosenbergi* – normally no more than two species are sympatric. Sexual dimorphism in size is evident in the smallest species (*"H. crepitans"*) but not in the others. All exhibit geographic variation in size, perhaps related to the combination of sympatric species of the group.

Key words. Amphibia, Hylidae, variability, new records, treefrogs.

RESUMEN

En Colombia se encuentran cinco especies de ranas gladiadoras (del grupo *Hyla boans*). *Hyla wavrini* apenas entra a Colombia (se encuentra en el límite oriental del país) e *H. rosenbergi* es endémica del Chocó biogeográfico. Las otras tres especies tienen distribuciones más amplias. *Hyla boans* se encuentra en el Chocó biogeográfico, Magdalena Medio y en la región cisandina por debajo de los 1000 m. *"Hyla crepitans"* se encuentra en el drenaje del Río Magdalena, así como en la parte occidental de los Llanos Orientales y con menor frecuencia en la región Caribe; la especie se distribuye desde el nivel del mar hasta un poco más de los 2000 m. *Hyla pugnax* se encuentra en las tierras bajas de la región Caribe, Magdalena Medio y también en algunos sitios de la Orinoquia, siempre por debajo de los 500 m. Es bastante común la simpatría entre *H. boans* e *H. rosenbergi* pero menos común entre *H. boans* e *"H. crepitans"* o *H. pugnax.* Se han registrado hasta tres especies simpátricas (*H. boans, H. pugnax* e *H. rosenbergi*) pero en general no coexisten más de dos especies. El dimorfismo sexual en tamaño es evidente en la especie más pequeña (*"H. crepitans"*) pero no en las otras. Cada especie muestra variación geográfica en tamaño, tal vez relacionada con la combinación de especies simpátricas.

Palabras clave. Amphibia, Hylidae, variabilidad, nuevos registros, ranas plataneras.

INTRODUCTION

Gladiator frogs are large, aggressive treefrogs distributed from Costa Rica to southern Brasil (Kluge 1979). Five species are known from Colombia: *H. boans, "H. crepitans", H. pugnax, H. rosenbergi,* and *H. wavrini,* but none is endemic. Lynch & Vargas (2000) reported the Colombian distribution of *H. wavrini,* a Guyana element that barely enters Colombia, being known from only Departamentos Guainía and Vaupés. The most recent summary of the gladiator frogs and their distributions in Colombia is by Kluge (1979) who concluded that *H. rosenbergi* was discontinuously distributed in the biogeographic Chocó, *H. pugnax* was a near-Colombian endemic, found in the Magdalena valley and along the Caribbean coast, *H. boans* was discontinuously distributed (biogeographic Chocó as well as Amazonia and the Orinoco, absent from the Magdalena valley), but was unaware that *H. wavrini* is a species distinct from *H. boans*, and that *"H. crepitans"* occurred in the Magdalena valley (and coastal lowlands) as well as in the upper parts of the Río Orinoco drainage. Because these are large conspicuous treefrogs of lowlands, Kluge (1979) presumed that absence of published records reflected absence of species, a conclusion we regard as premature. We have little to add to the published record as concerns *H. rosenbergi* and *H. wavrini*; our study concerns primarily the other three species (*H. boans, "H. crepitans", and H. pugnax*).

The theory of sexual selection places a good deal of attention on sexual dimorphism (here in terms of size). Kluge (1979) noted that his material of *"H. crepitans"* supported the view that males were smaller than females whereas males and females of the other species (that he recognized) were of equal sizes (an observation consistent with sexual selection). So far as is known, among frogs of the *H. boans* species group, there is marked aggression among males for the possession of a breeding site. Nevertheless, this does not translate into a bias in size for males in the *H. boans* species group. Over the past thirty years, biologists from the Instituto de Ciencias Naturales of the Universidad Nacional have descended into the lowlands on many occasions and, whenever the opportunity presented itself, have collected gladiator frogs. These are rather large treefrogs and therefore conspicuous (which does not always translate into vouchers). Both *"H. crepitans"* and *H. pugnax* are known locally as *ranas plataneras,* meaning that neither local biologists nor *campesinos* distinguish the two species. Beginning in 1980, efforts were made to document distributions, ensuring at least one voucher per locality (but one specimen is not adequate to test the proposition of sympatry). Given that local biologists did not distinguish the species and that each species is locally abundant, the database available to us is diminished because most potential collectors did not bring specimens to ICN (reasoning, perhaps, that enough specimens were available already and acting "ecologically"). Relatively little of the available data have been published (excepting Lynch & Vargas, 2000) and the data available require a more complicated view that that presented by Kluge (1979), offering many options to students who wish to confront a variety of issues in ecology and reproductive biology.

MATERIALS AND METHODS

Our study of these frogs is based on the study of more than 700 specimens available from the Instituto de Ciencias Naturales (ICN) and the Instituto Alexander von Humboldt (formerly the collection of INDERENA) (IAvH). For each specimen, we recorded sex, size, maturity, a few morphological characters (pigmentation of the lower eyelid, calcar development, degree of webbing of the hand, degree of webbing of the foot, and color pattern data), and locality. Means are reported ± 1 standard error of the mean.

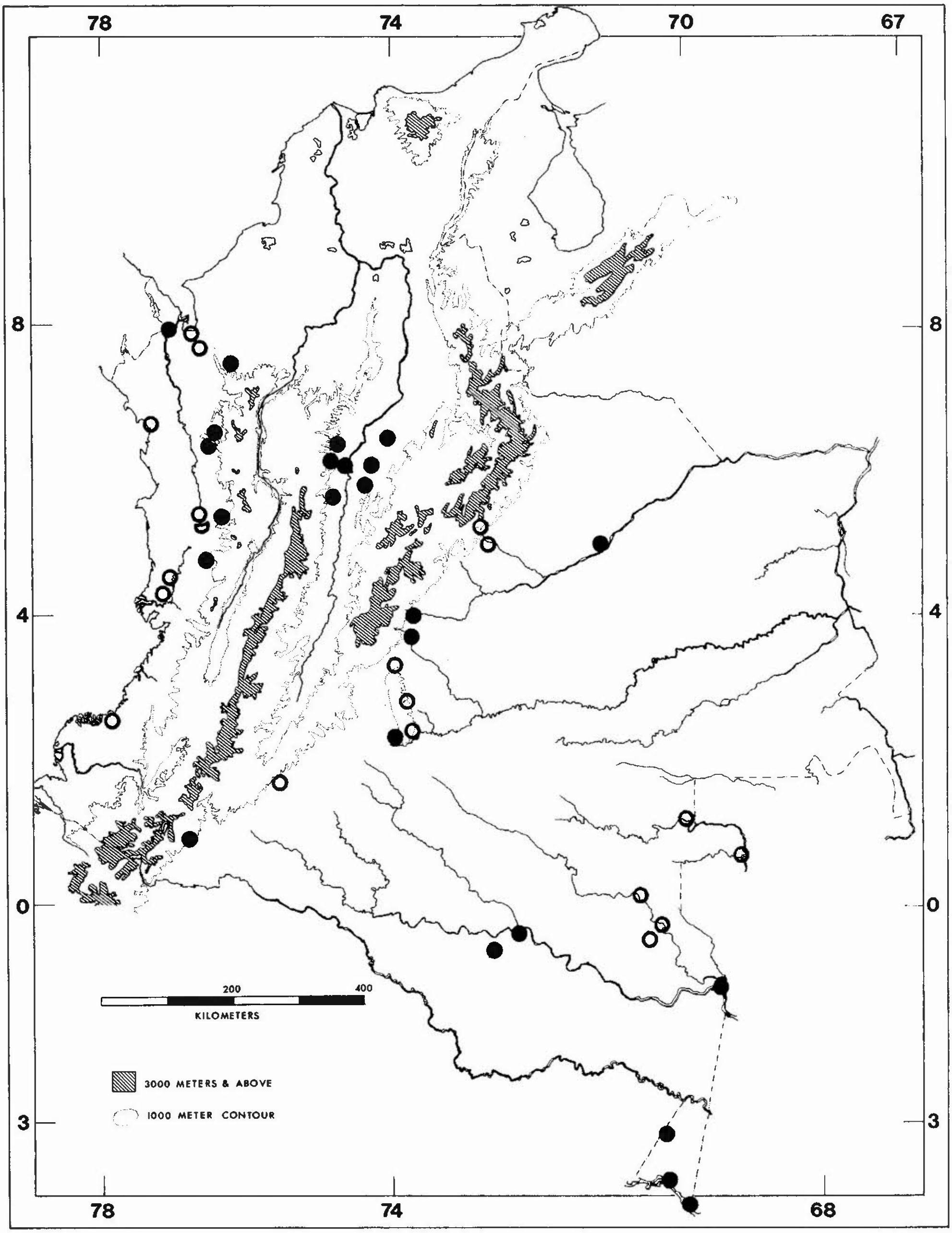
RESULTS

Both sexes of these species exhibit angled vomerine odontophores (a trait shared by few other *Hyla,* but also by some excluded genera, such as *Osteocephalus*) and adult males possess a protuberant prepollex (shared by a few other groups of *Hyla,* some of which also exhibit angled vomerine odontophores). All species, for which tadpoles are known, possess a larval tooth row formula of 2/4. Although Kluge (1979) thought that this combination might be sufficient, we are not sanguine that the *Hyla boans* group is monophyletic (in the face of the available data and arguments).

Only *H. boans* exhibits an obvious calcar. That species as well as *H. wavrini* exhibits a reticulum in the lower eyelid (a feature shared by *H. geographica* and *H. microderma* of the *H. geographica* group). Each of the species of the *H. boans* group exhibits geographic variation in size of adults (and, presumably, age at maturity) but this is minimal in *H. pugnax*. *Hyla wavrini* has significantly reduced manual webbing (but cannot be confused with the small species of the group, whose manual webbing is very reduced). *Hyla rosenbergi* is an only slightly smaller treefrog, also with extensive webbing of the hands. Unlike the other two large species (from a Colombian perspective), it lacks a reticulum on the lower palpebrum (rather pigment is distributed uniformly). The other two species are smaller and have reduced webbing of the fingers (not reaching the disks nor extending past the ultimate subarticular tubercle of Fingers III or IV). The lower palpebrum of *H. pugnax* lacks pigmentation whereas the anterior half of the palpebrum of *"H. crepitans"* is pigmented. The two species can be distinguished as well because *"H. crepitans"* is a smaller frog (see species account), has less webbing of the fingers and toes, lacks barring on the anterior face of the thighs, and has simple flank barring (Kluge 1979). Kluge (1979) suggested that webbing characters were unreliable when dealing with juveniles. In our experience, the flank and thigh pigmentation patterns are unreliable when dealing with juveniles but the palpebral pigmentation patterns are not influenced by size or age.

Hyla boans (Linnaeus)

Kluge (1979) was perplexed by the variance of size of this species. However, Lynch & Vargas (2000) asserted that cis-Andean Colombian populations differed markedly in adult size (populations from the Orinoco are significantly smaller frogs than those from Amazonia). Kluge (1979) also opined that the absence of records from the Magdalena drainage did not reflect collecting effort. We beg to disagree but are uncertain when the first *H. boans* was collected in the Middle Magdalena, although JDL collected specimens in eastern Caldas in 1981. One might quibble that the report from southern Córdoba (Renjifo & Lundberg 1999) hardly represents a distribution outside of the biogeographic Chocó (a view with which we agree) but the records from eastern Antioquia, eastern Caldas, and western Boyacá, Cundinamarca, and Santander reflect a Middle Magdalena distribution (Fig. 1), a pattern reinforced by such taxa as *Bufo haematiticus, Hyalinobatrachium colymbiphyllum,* and *Hyla palmeri*. Minimally, *H. boans* is distributed in the biogeographic Chocó and Nechí districts (following Müller 1973) of Colombia, as well as the connecting terrain.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KILOMETERS
3000 METERS & ABOVE
1000 METER CONTOUR

Figure 1. Distribution of *Hyla boans* in Colombia. Solid symbols represent localities for specimens examined. Open symbols represent literature records (Kluge 1979).

In the collections of ICN, there are only 12 males from the biogeographic Chocó (76.9 – 107.6 [mean 87.8 ± 2.3] mm SVL and three females [82.5-97.1, mean 89.7] mm SVL). These are notably smaller than the frogs reported by Duellman (1970) from eastern Panamá. The sample from the interior (Middle Magdalena, excluding the headwaters of the Río Sinú) consists of 20 males, five females, and three juveniles. The males are 68.9 to 95.3 (mean 81.6 ± 1.7) mm SVL, the ovigerous females are 70.8 to 84.2 (mean 77.0) mm SVL and the juveniles 45.6 to 58.6 mm SVL. The samples are minimal, but it would appear that specimens of *H. boans* from the Middle Magdalena are smaller than those from the Chocó (and Panama, following Duellman 1970, and Kluge 1979)-adding to the geographic variation in sizes of adult of *H. boans* reported by Lynch & Vargas (2000).

In Colombia, *H. boans* occurs at elevations below 1000 m and we suspect that it is distributed continuously along the biogeographic Chocó (Panamá to northwestern Ecuador), across the northern fringes of the cordilleras Occidental and Central into the Middle Magdalena and then discontinuously (due to the elevations of the Cordillera Oriental) into the eastern lowlands (Fig. 1). Combining our data with that of Lynch & Vargas (2000), large frogs occur in the biogeographic Chocó and in the drainage of the Río Amazonas but smaller *H. boans* occur in the Middle Magdalena and western Orinoco.

In the biogeographic Chocó, *H. boans* is sympatric with the slightly smaller *H. rosenbergi*, a fact that may explain its large size there (under the assumption that these two compete for some resource, perhaps a foolish assumption, because this argument does not account for equally large specimens from Amazonia, where *H. boans* is not sympatric with another large species of the group). *Hyla rosenbergi* is poorly represented in the ICN collections but occurs in southern Córdoba as well as the biogeographic Chocó (Costa Rica to western Ecuador, Boulenger 1898, Cochran & Goin 1970, Duellman 1970 and Kluge 1979). At least in the Middle Magdalena, *H. boans* co-occurs with either *"H. crepitans"* or *H. pugnax*, each of which is a markedly smaller frog than *H. boans* (even considering that the Middle Magdalena *H. boans* are small in comparison with populations in western Colombia, Panama, or Ecuador).

"Hyla crepitans" **Wied**

Like Kluge (1979), we cannot assert that this species is the same as that described by Wied (1824) from extreme eastern Brasil (Bahía). That caveat given, we will refer to the smallest Colombian species of the *H. boans* group as *"H. crepitans"*. In Colombia, *"H. crepitans"* occurs as high as 2450 m (western Santander) and there are many records above 1000 m on both flanks of the Cordillera Oriental. The lowest altitudinal record is 5 m (Puerto Colombia, Atlántico). The species is abundant in the middle and southern portions of the Magdalena drainage and normally scarce (meaning that we have few records as vouchers) towards the Caribbean coast. The distributional disjunction (absence in eastern Panamá and western Colombia) noted by Kluge (1979) appears to be real (we are aware of no records to the west of the Golfo de Morrosquillo in Colombia, an area with relatively few vouchers).

Kluge (1979) emphasized that *"H. crepitans"* was rarely sympatric with *H. pugnax*, and that it never co-occurred with both *H. pugnax* and *H. rosenbergi* (something that would require observation in central Panama, where he worked, under our assumption that *"H. crepitans"* is discontinuously distributed in northwestern Colombia and Panamá). In Colombia, three gladiator frogs (*H. boans, H. pugnax*, and *H. rosenbergi*) co-occur in the headwaters of the Río Sinú and in the Parque Nacional Natural de Katios in the northern Chocó, otherwise, no more than two are sympatric (although localities for three, *H. boans,* *"H. crepitans",* and *H. pugnax,* are spaced very closely in eastern Caldas). In Colombia, *"H. crepitans"* is never sympatric with *H. rosenbergi* and appears to rarely be sympatric with *H. boans* (two occurrences, Municipio Yacopí, Cundinamarca, and at Orocué, Casanare, as well as Kluge's [1979] report from either extreme eastern Boyacá or adjacent Meta, at Guaicaramo). Kluge (1979) reported *"H. crepitans"* from 28 trans-Andean localities in Colombia and, for two of these, noted sympatry with *H. pugnax.*

Our observations (hundreds of hours of casual observation on the part of JDL during the past 22 years, supported by the recalled observations of the late Pedro M. Ruiz, *pers. comm.*, and our consultation of fieldnotes available in the Laboratorio de Anfibios, ICN) of these two species suggest that they differ ecologically in that *"H. crepitans"* nearly always calls from the ground (like *H. rosenbergi*, based on JDL's recalled observations in western Ecuador) whereas *H. pugnax* calls from shrubs or trees (like *H. boans* and *H. wavrini,* although once a nest is made or selected, *H. boans* and *H. wavrini* can be found calling from the ground as well). We must emphasize that these observations were casual, and are perhaps mistaken, but suggest some behavioral difference, not noted previously, between these two species.

The trans-Andean records (from Colombia) available to us reinforce Kluge's assertion – that sympatry of *"H. crepitans"* and *H. pugnax* is rare or non-existent. At a coarse-grain level, the two are sympatric in the Parque Tayrona (Depto. Magdalena) — but the park is a large geographic unit and JDL's experience in 1983 revealed only *"H. crepitans"* in three weeks of fieldwork (and see below) – and Kluge's (1979) reports for two localities in Depto. Magdalena (and five records reported here, two in Depto. Arauca one in Depto. Caldas, and two in Depto. Sucre). Collecting/ observation on the part of JDL in and around the campus of the Universidad de Magdalena (just S of Santa Marta) revealed only the presence of *H. pugnax* (2-3 weeks of observation in 1998 and 1999) as did 10 days of fieldwork at El Ceibal (Municipio Santa Catalina) in northern Bolivar in October 2000 and one night of fieldwork in southern Depto. Atlántico in October 2000 – and at two localities in cis.-Andean Arauca (but see below). Hundreds (or thousands) of *H. pugnax* were heard/ observed but not one *"H. crepitans"* during fieldwork at El Ceibal, Polonuevo, and just south of Santa Marta. These observations do not contradict the claim (Kluge, 1979) that the two species are/ were sympatric, in the early 1920's, at Finca El Aranar, near Bonda or at Fundación (both in Depto. Magdalena), based on the fieldwork of Alexander Ruthven, but we suspect that in each case a macrogeographic perspective has obscured the actual distributions of the two species. In the 1910s and 1920s, a finca (El Aranar) or a town (Fundación) presumably covered an area with a diameter measured in kilometers (not allowing a test of our suggestion that these two species are never microsympatric). Taking locality data at face value, without reference to the collector's fieldnotes, also provides the illusion of sympatry at two localities in Depto. Arauca (Orinoquian Colombia). Kluge (1979) reported *H. pugnax* from Girardot (Depto. Cundinamarca) and from Espinal and Honda (Depto. Tolima) in the Magdalena valley, just west of Bogotá. We have experience at Nilo (Depto. Cundinamarca) and at Venadillo (Depto. Tolima), geographically intermediate sites, where we observed/ heard only *"H. crepitans".* The records from Depto. Sucre involve specimens taken by different collectors in different years. The only locality for which sympatry seems certain is in Dept. Caldas (ICNMHN 34533-38, *H. pugnax,* and 34548-51, *"H. crepitans"*) where both species were collected in a pasture on 23 March 1994.

Hyla crepitans occurs from the Caribbean coast to the upper Magdalena valley at elevations between sea level and more than 2400 m. In the Parque Nacional Natural Tayrona (Depto. Magdalena), *"H. crepitans"* builds nests made of small diameter gravels (Lynch & Vargas, 2000) but otherwise it deposits its floating egg film on the surface of ponds (pers. observations at sites above Cañaverales, Magdalena, as well as at Venadillo, Tolima, and in the vicinity of Villavicencio, Meta). ICNMHN 33115 (*H. pugnax*) is recorded from "Cañaverales," a site a few meters above sea level. In 1983, JDL did not collect at Cañaverales (the staging site for the Segunda Expedición Botánica) but did collect at the slightly higher El Cedro, where only *"H. crepitans"* were found/ observed. These localities are separated by only a few kilometers. Maps of the scale used here and by Kluge (1979) provide the illusion of sympatry. No records are available for this species from the drainage of the Río Cauca (a pattern repeated by most species of the Caribe/ Río Magdalena pattern). The species also is found along the piedmont of the departments of Arauca, Casanare, and Meta to the east of the Andes and in the southwestern edge of the drainages to Lago Maracaibo in Venezuela (Fig. 2). Given that the species can occur above 2000 m, the Táchira depression of western Venezuela is not a barrier (a second pass is available just N of Picachos [Caquetá – Huila], enabling contact between the populations of the Magdalena and Orinoco) . The eastern limits of distribution remain to be described. Personnel from ICN have rarely collected the llanos at any distance from the Cordillera Oriental and the most eastern localities of gladiator frogs suggest the presence of *H. pugnax,* not *H. crepitans* (see below), a further issue for study.

Kluge (1979) noted that *"H. crepitans"* is the smallest of the species of the *H. boans* group and noted that some geographic variation in size is apparent. Our data suggest that geographic variation in size is much more complex than suggested by Kluge (1979), who found that the trans-Andean Colombian populations (59 males, 14 females) were smaller frogs than those from Panamá (31 males, 9 females) and the Orinoco (27 males and 14 females). Our measurements of 228 adult males and 54 adult females (from Colombia) in general confirm Kluge's (1979) claim that *"H. crepitans"* from the Llanos are larger than those from the Caribbean/ Magdalena (Table 1). That said, there are significant differences in size among adults from Meta as contrasted with those from slightly higher elevations in Boyacá and Cundinamarca or those from the lowlands of Arauca and Casanare. In general, frogs from trans-Andean Colombia are smaller than those from cis-Andean Colombia but the small sample available from southern Tolima consists of frogs as large as those from cis-Andean Colombia.

Other than sizes of adults, Kluge (1979) distinguished *"H. crepitans"* and *H. pugnax* using webbing of the hands (the membrane does not reach the distal subarticular tubercles in *"H. crepitans"* and does in *H. pugnax*), lower palpebral pigmentation (anterior half in *"H. crepitans"*, only the dorsal edge in *H. pugnax*), two characters of pigmentation (anterior thigh with bars in *H. pugnax* but not in *"H. crepitans"*, flanks with prominent vertical bars, often doubled, in *H. pugnax,* whereas the barring is tenuous and simple in *"H. crepitans"*) and calls (a feature obvious to anyone with experience with each species). In addition, we noticed that *"H. crepitans"* has generally less webbing of the interior toes than does *H. pugnax* (Fig. 3), an observation expected, given than webbing of the hand is correlated with webbing of the foot.

Hyla pugnax Schmidt

Kluge (1979) pointed out that Duellman (1970) erred in considering this a synonym of *"H. crepitans"* and declared it a near-endemic of Colombia. He reported it from 30 trans-Andean Colombian localities and one in the Colombian Amazon (not mapped, nor commented upon), saw a few (6) Panamanian specimens (including the holotype), and disputed a record from relatively high altitudes (Garagoa, Boyacá) in the Amazonian versant. We agree

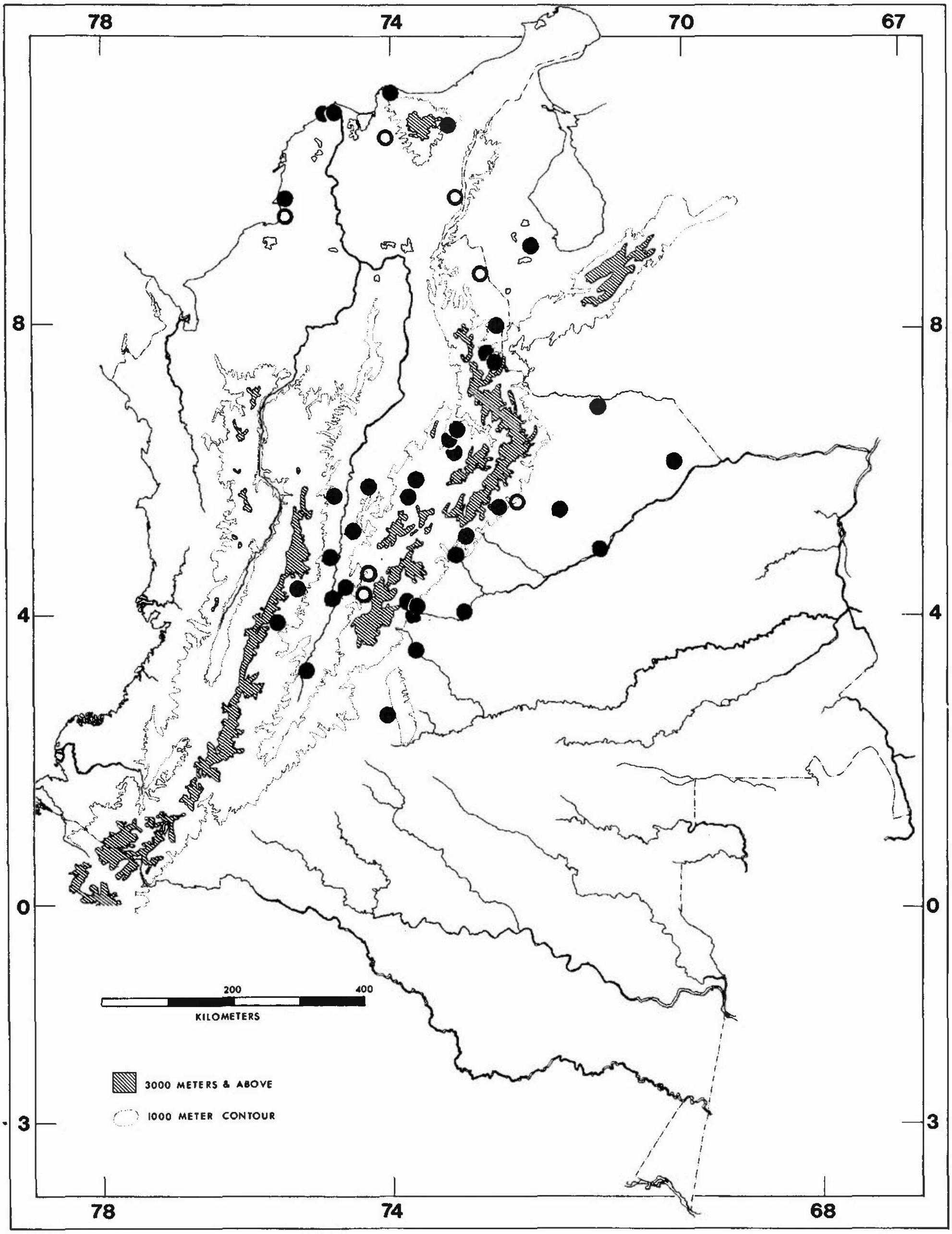
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Figure 2. Distribution of *"H. crepitans"* in Colombia. Solid symbols represent localities for specimens examined. Open symbols represent literature records (Kluge 1979).

with his skepticism concerning the Garagoa record, in part because we have taken *"H. crepitans"* in the Garagoa area and doubt that *H. pugnax* occurs at such elevations. *Hyla pugnax* is widely distributed in the lowlands (below 500 m) of the Caribbean region of Colombia and the Magdalena valley but is also found in western Venezuela and in the Orinoco of Colombia (Fig. 4). The records from the Caribbean coast and the Magdalena valley provide an altitudinal range of *H. pugnax* between 5 and 450 m aside from one record (Minca, Depto. Magdalena, above 1500 m, that we question/ reject). The present elevations of the Táchira depression greatly exceed the altitudinal range of *H. pugnax* (see below) but we presume that Pleistocene effects allowed communication of populations between cis and trans-Andean South America.

The available data require that we view *H. pugnax* as a low-elevation treefrog (below 500 m) but we are unable to explain why this species should be restricted to very low elevations. It may be that *H. pugnax* (in contrast to *H. crepitans*) is unable to breed in the cooler environments above 500 m (a proposition easily tested under laboratory conditions). Reviewing fieldnotes (deposited in the laboratory of amphibians, ICN) suggests that *H. pugnax* may be more inclined to utilize waters associated with streams that *H. crepitans* (mostly a denizen of ponds, but not in the Sierra Nevada de Santa Marta). If we are correct in accepting this supposition, then the difference in altitudinal ranges of the two species is difficult to explain (one might expect *H. pugnax* to enjoy a greater altiudinal distribution/ range than *H. crepitans*, stream habitats being more normal

Table 1. Geographic variation in sizes of adult *"Hyla crepitans"* in Colombia. The first line reports the range and sample size, the second line the mean ± 1 standard error of the mean.

	Males	Females
Arauca - Casanare	51.3—64.6 (29) 55.9 ± 0.5	50.5—66.4 (10) 61.1 ± 1.4
Eastern Boyacá/ Cundinamarca	47.6—60.5 (23) 54.0 ± 0.7	58.2—61.0 (3) 60.0
Meta	45.5—56.0 (55) 51.6 ± 0.4	52.3—62.4 (8) 57.9 ± 1.4
Cesar	47.7—54.5 (4) 50.8	53.7—56.7 (2)
Magdalena	46.4—57.3 (29) 52.3 ± 0.5	54.1—61.5 (15) 58.1 ± 0.6
Charalá/ San Gil, Santander	43.0—52.7 (13) 47.4 ± 0.9	51.0—54.1 (3) 53.0
San José de Suaita, Santander	43.2—50.6 (30) 47.2 ± 0.3	54.0—57.0 (4) 55.6
Western Boyacá/ Cundinamarca	46.3—51.7 (10) 48.6 ± 0.6	53.2—62.6 (6) 57.6
Caldas	40.8—52.3 (17) 49.7 ± 0.7	
Northern Tolima	48.8—56.4 (2)	52.8—55.5 (2)
Southern Tolima	50.7—58.7 (11) 54.7 ± 0.8	62.6
Huila	45.5—48.1 (5) 47.0	57.8

at elevation than are pond habitats) – as a result of this observation, we suspect that temperature plays a greater role than altitude (even though the two are grossly correlated, a suggestion that merits testing under laboratory control).

In contrast to *"H. crepitans"*, *H. pugnax* is nearly invariate in size (between sexes and between localities). Kluge (1979) asserted that mean sizes of males and females were not distinguishable statistically and our study of samples from Bolivar (two localities), Boyacá, Cesar, and Córdoba, agree fully with his position, even though there are significant differences (perhaps artifacts of sample sizes) between sizes at different localities (Table 2).

The differences in altitudinal distributions (*H. crepitans* at 5-2450 m and *H. pugnax* at 5-450 m) mean that, at many localities, only *H. crepitans* might be found but, that all localities for *H. pugnax* potentially allow for sympatry (within the biogeographic unit west of the Cordillera Oriental, as well as the Maracaibo Basin). In spite of this observation, we remain impressed by the near absence of sympatry (the absence, based on our experiences) between *"H. crepitans"* and *H. pugnax* (recall our comments above). Reinforcing this position is the discovery of different species at localities very near one another in the absence of some obvious difference in climate or vegetation. In the upper part of the valley of

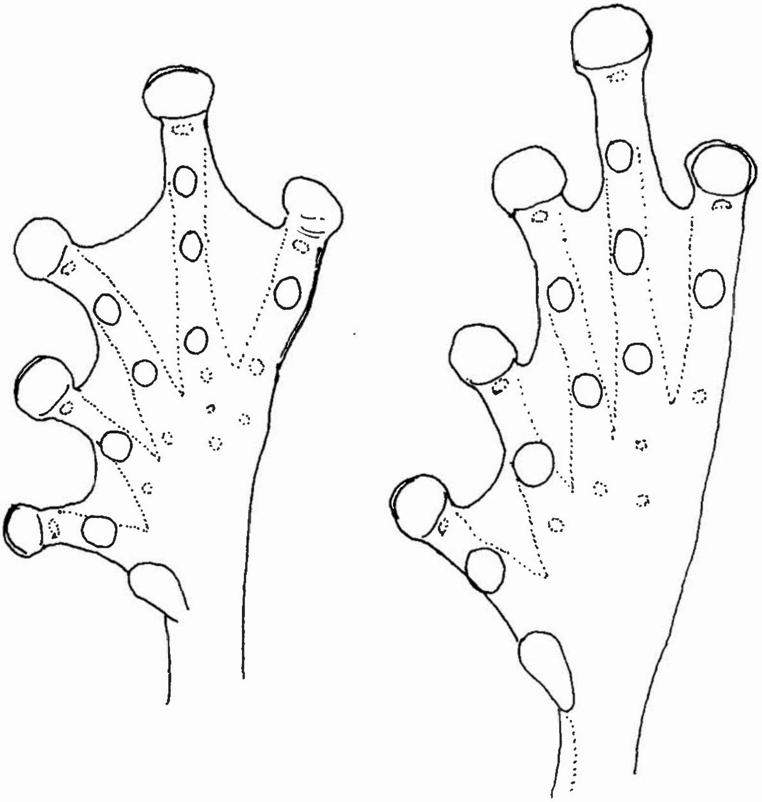

Figure 3. Plantar views of feet of *"Hyla crepitans"* (left, ICNMHN 40835) and *H. pugnax* (right, ICNMHN 44440) showing difference in webbing between inner two toes. The difference is best described as *"H. crepitans"* has more deeply incised webbing between toes I and II.

the Río Magdalena (Fig. 5), combining our data with those of Kluge (1979), *"H. crepitans"* and *H. pugnax* display a checkerboard pattern of distribution below 500 m (if one is present, the other is absent). We are unable to cite any ecological difference between such sites as Espinal, Girardot, and Honda in contrast to Carmen de Apicalá, Melgar or Venadillo while the first three harbor *H. pugnax* and the last three *"H. crepitans"*. In 1992, JDL collected frogs in the southwestern edge of the Maricaibo Basin (Norte de Santander). There was no obvious difference between sites within the perimeter of Astillero and a site 4.3 km to the north of that town yet the former harbored only *H. pugnax* (by examination of specimens and calls) and the latter harbored only *"H. crepitans"* (by examination of specimens and calls). These data as well as the observations of JDL in Atlántico and Bolivar in 2000 and those in Magdalena in 1998-99 suggest to us that *"H. crepitans"* and *H. pugnax* do not cooccur (*contra* the reports of **Kluge** [1979] and *contra* our reports of sympatry [based on examination of museum specimens] at San Luis de Onofre, Córdoba, Coloso, Sucre, and a locality in western Venezuela). A single case of sympatry is apparent to us.

Why *"H. crepitans"* and *H. pugnax* should be nearly mutually exclusive geographically requires serious investigation in more than one of the areas within the zone of potential sympatry (Caribbean coast and Magdalena valley). The near-absence of sympatry suggests some sort of competitive exclusion although we are unable to offer an hypothesis at this time.

Hyla rosenbergi Boulenger

We are not so sanguine as Kluge (1979) to suggest that this species exhibits a discontinuous distribution along the western coast of Colombia. Few biologists have made collections in the biogeographic Chocó and the gaps can be explained as well for failure to make collections as for absences. In the absence of data to the contrary, we expect that *H. rosenbergi* enjoys a continous distribution from central Panamá to western Ecuador (*contra* Kluge, 1979). The record in the southern part of Depto. Córdoba extends the biogeographic Chocó slightly to the east.

Table 2. Size variation of adults of *Hyla pugnax*.

	Males	Females
Santa Catalina, Bolívar	53.6—75.6 (28) 66.9 ± 1.2	65.0—75.2 (5) 70.8
Santa Rosa, Bolívar	63.1—74.6 (31) 68.5 ± 0.6	64.3—74.2 (14) 68.4 ± 0.8
Western Boyacá	56.7—72.6 (28) 66.3 ± 0.8	64.9—67.1 (5) 66.3
Caldas	66.8—72.9 (6) 69.8	
Cesar	62.2—65.6 (4) 64.2	65.6
Southern Córdoba	65.5—77.5 (11) 71.4 ± 1.1	67.4—75.7 (4) 72.4
Norte de Santander	60.7—72.3 (7) 68.0	

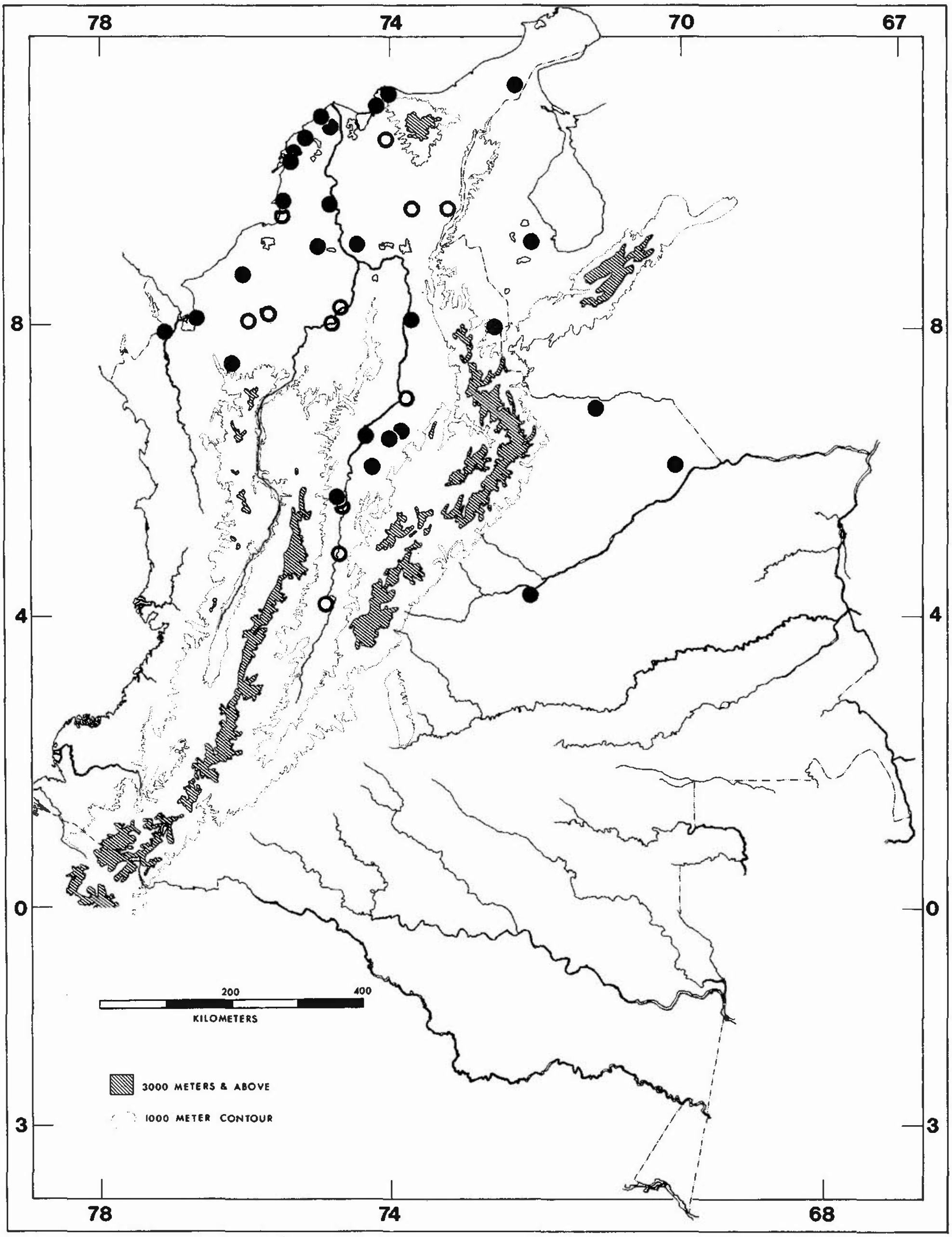
78
74
70
67
8
8
4
4
0
0
3
3
78
74
68
200
400
KILOMETERS
3000 METERS & ABOVE
1000 METER CONTOUR

Figure 4. Distribution of *Hyla pugnax* in Colombia. Solid symbols represent localities for specimens examined. Open symbols represent literature records (Kluge 1979).

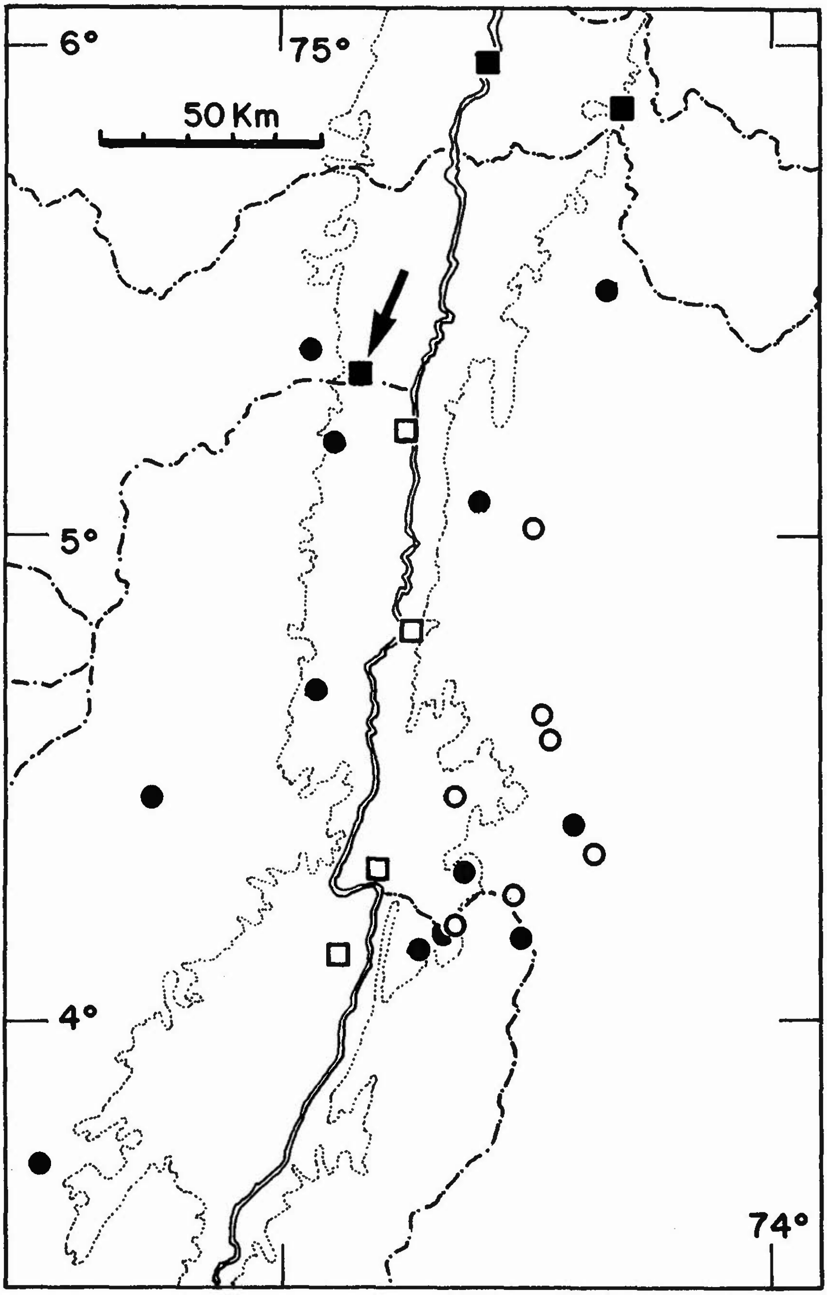

Figure 5. Distributions of *"Hyla crepitans"* and *H. pugnax* in the Upper portion of the Río Magdalena (Deptos. Boyacá, Caldas, Cundinamarca, and Tolima). Circles represent *"H. crepitans"* and squares *H. pugnax*. Solid symbols represent localities for specimens examined. Open symbols represent literature records (Kluge 1979). An arrow indicates the locality of sympatry. The 500 m contour is indicated by dotted lines.

***Hyla wavrini* Parker**

We have nothing to add as concerns this Guayanan species to what was published recently by Lynch & Vargas (2000), who related that it exhibited geographic variation in size (for reasons unfathomed) and could be found in Guainía and Vaupés in Colombia (at the latter, in sympatry with *H. boans*).

DISCUSSION

The central position, one not at variance with the previously published position (e.g., Kluge, 1979) is that there exist, in Colombia, five species of gladiator frogs. We disagree, in a small way, with Kluge's (1979) assertions concerning the exact distributions of these species but recognize that we have the advantage of time and more specimens than did he.

That said, we do disagree at a much more fundamental level concerning certain points about gladiator frogs. Kluge (1979) opined that adults of *H. boans, H. pugnax,* and *H. rosenbergi* did not differ in size (geographically or sexually). In this we must disagree. We concur with Lynch & Vargas (2000) that the size difference observed between Amazonian and Guyanan *H. boans* is not trivial and that it appears that *H. wavrini* also exhibits geographic variation in size (Lynch & Vargas, 2000). Whether or not *H. rosenbergi* actually exhibits geographic variation in size will require better samples than those available to Kluge (1979), or to us.

Those points made, we agree with Kluge (1979) that there is no detectable (by size) sexual dimorphism between sizes of *H. pugnax.* This point applies as well, in our experience, to *H. boans* and *H. rosenbergi.* Female treefrogs are rare at breeding congresses where collectors make their collections. Their rarity results from the variables that govern the reproductive cycles of an individual female. Crump (1974) pointed out that individual females might return to the breeding site (a lek) every month in an aseasonal climate. Frogs of the *H. boans* group live in mostly seasonal climates (pronounced wet and dry seasons). In parts of the biogeographic Chocó and Amazonas, the climate, from a frog's point of view, is aseasonal but in the remaining parts, the climate is seasonal. That said, most collections consist of inadequate samples of females to test the proposition that there are size differences between females from different localities.

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APPENDIX I (SPECIMENS EXAMINED)

HYLA BOANS (49, trans-Andean, see also Lynch & Vargas, 2000)

Chocó biogeográfico

Antioquia, Frontino, Vereda Venados, 950-1060 m (ICN 19481); Puerto Palacios, Río Arquia, 50 m (ICN 578). **Chocó**, Lloro (ICN 16655-57), limite con Risaralda; Parque Nacional Natural de Los Katíos (4 uncatalogued); Km 20.6 carr. Santa Cecilia a Quibdo (ICN 27518), 2.5 km SW San Jose del Palmar (ICN 41296-97).

Middle Magdalena

Antioquia, Puerto Triunfo, 500 m (ICN 39371); San Carlos, 970 m (ICN 39373); San Luis, 320 m (ICN 15816, 39372). **Boyacá,** Puerto Boyacá, inspección de policía Puerto Romero, Vereda La Fiebre, quebrada La Fiebrecita, 300 m (ICN 38068-69, 44555). **Caldas,** La Victoria, Km. 35 carr. La Dorada-Sonsón, 520 m (ICN 9264-65). Norcasia, Quebrada El Diamante, 600 m (ICN 45141-42), Río La Miel, 640-660 m (ICN 34575-76), Vereda Corinto, 450 m (ICN 43516-21), Vereda La Miel, 500 M (ICN 45144-47), via Berlin, 2.2 km de Norcasia (ICN 451439, via Norcasia-Puente Hierro, 5 km, 480 m (ICN 45148). **Córdoba,** Tierra Alta, Vereda Caña Fina, 130-180 m (ICN 39222-23), Quebrada La Mina, 120-135 m (ICN 39224), Represa Urrá (ICN 43414-15, 4 uncatalogued). **Cundinamarca,** Yacopí, inspección de policia Guadualito, Vereda Barbascales (ICN 42925). **Santander,** Landázuri, Hda. Las Flores, Quebrada. Pinilla, 450 m (ICN 8715, 31763).

HYLA CREPITANS (343)

Atlántico, Barranquilla (ICN 41756); Puerto Colombia, Prado (ICN 253-54). **Arauca**, Arauca, Hato El Venero, IAvH 3903-04; Finca La Yuaful (ICN 13785); Caño Limón, Yarumal via Matanegra (ICN 26733, 26736); Relleno Sanitario (ICN 27193-94, 27648-54, 27791-805); caño Limón y Caño Otilia (ICN 27654-55); Sector facilitador de producción, campamento El Limonar (ICN 27195-96). **Boyacá**, Miraflores, Vereda El Tunjito, 1780 m (ICN 22444-45); Pajarito, casco urbano (ICN 533-54), Corinto, Quebrada Las Jotas, 1600 m (ICN 8516); Santa María, Quebrada. La Cristalina, 800 m. (ICN 40660); Santa María, Vereda. Ceiba Chiquita, Quebrada. La Clarita, 780 m. (ICN 40658-9); Santa María, Vereda. Culima, carr. Sta. María - Mámbita, 520 m. (ICN 40661-6, 44799-808); Santa María, sendero hacia Quebrada. Las Moyas, 1100 m. (ICN 40667); Togüí, Vereda Versalles, 1600 m (ICN 1382, 5981-82). **Caldas**, La Victoria, Km 15.6 carr. La Victoria a la central (ICN 34548-51); Norcasia, campamento Tasajos, Quebrada Tasajos at Río La Miel, 530 m (IAvH 6265, ICN 34539-47); Norcasia, Vereda La Estrella (ICN 40241), campamento CHEC, proyecto Miel II (ICN 40242-45, 40262-63). **Casanare**, Orocué

(ICN 44611-15); San Luis de Palenque (ICN 2638). César, Valledupar, Pueblo Bello (ICN 35188-93). **Cundinamarca**, Guaduas, Vereda Santa Rosa (ICN 5980); Guayabetal, casco urbano (ICN 9745); Nilo, casco urbano, 450 m. (ICN 12999); Silvania, El Bosque (ICN 35127); Ubalá, Insp. Mámbita, casco urbano, 820 m. (ICN 40829-31), Vereda. Boca del Monte, 1100 m. (ICN 40832-34, 41215-18), , Vereda. Boca del Monte, ventana Z. (ICN 40835), Vereda. Pto. Solla, margen izquierda. río Zaguea, 500 m. (ICN 41219); Yacopí, Inspección de policía Guadualito, Vereda Cabo Verde, 1100 m (ICN 42888, 42895), Vereda El Lamal, 1100 m (ICN 42885-87, 42889, 42894), Vereda Sardinas, finca Mantecaña, 1120 m (ICN 42890-93). **Huila**, Villavieja, Quebrada La Batea (ICN 11678); 10 Km carr. Villavieja a Baraya, 530 m (ICN 11679-81); Vereda Los Hoyos, 300 m (ICN 36618-19). **Magdalena**, Sta. Marta, Minca - Cincinati, 1530 m. (ICN 3777-8, 3960); Sta. Marta, PNN Tayrona, 360 - 400 m. (IAvH 2041-42, 2044-46, 2444, 2580-84, ICN 13704); Sta. Marta, PNN Tayrona, cabaña El Cedro, 360 m. (ICN 13626, 13629-30, 13669-86, 13688-97, 26215-7, 26243-49, 26251-6); Sta. Marta, PNN Tayrona, Quebrada. El Cedro, 500 m. (ICN 11450-6, 26218-23, 26257-9); Sta. Marta, río Guachaca, 680 m. (ICN 20337-43). **Meta**, Acacías, Vereda. San José, 670 m. (ICN 14172, 14174-7), Vereda. San Juanía, río Orotoy, 850 m. (ICN 14173), Vereda. Vista Hermosa, 1000 - 1080 m. (ICN 39422, 39424-6); Cubarral, El Dorado. (ICN 39440, 39490), Km. 8 carr. Cumaral – Paratebueno. (ICN 21278-9); Cumaral, Hda. La Alcancía. (ICN 21281-3), laguna en el desvío Veracruz - San Nicolás. (ICN 36300-1); Fuente de Oro, Vereda. La Esperanza. (ICN 23100-9); Guamal, Hda. Avichure, 550 m. (ICN 14178-9); Parque N. N. Macarena, Río Duda (ICN 21492); Puerto López, Hda. Mozambique. (ICN 1338, 2392-4, 35804); Restrepo, 3 Km. N Restrepo, 740 m. (ICN 5029), CREAD. (ICN 17315-7), Km. 10 desvío a San Nicolás. (ICN 17318-20, 36262); Villavicencio, carretera del amor. (ICN 2416-7), casco urbano. (ICN 2454-7, 5749), Hda. Las Brisas. (ICN 20498, 20514-20), vivero Campo Alegre. (ICN 20586-7), vivero Mesetas. (ICN 20627-32), puente sobre el río Guatiquía. (ICN 26281-2), Vereda. Argentina. (ICN 36302-3), Vereda. Las Mercedes, caño Candelaria, 480 m. (ICN 39423), Km. 8 carr. V/vicencio - Acacías, 580 m. (ICN 39427-8), Km 16 carr. Villavicencio—Pto. López, Hda Potreritos, IAvH 4659-61. **Norte de Santander**, Astillero, 4.3 km N Astillero, 260 m (ICN 33548) Chinácota, Vereda Paramito, 5 km S Chinácota, 1390 m (ICN 15008), 3-5 km S Chinácota, 1390-1440 m (ICN 15009); Zulia, 13 km S Zulia, 300 m (ICN 33571). **Santander**, Charalá, Virolín, finca Alianza (ICN 11276), Vereda cañaverales, Río Luisito, 1700 m (ICN 7382-83, 33144-47), Vereda El Reloj, 1740-1750 m (ICN 4499, 5108-09); Gámbita, Bogotacito, Km 55-56, carr. Duitama-Charalá, 2400 m (ICN 12591), Vereda El Taladro, Km. 55-57 carr. Duitama – Charalá, 2450 m (ICN 11092); San Gil, 7 km SW San Gil, carr. a Socorro, 1180 m (ICN 22446); Socorro, Hda. La Esmeralda (ICN 1426), Hda. Palermo, 1700 m (ICN 1346). **Sucre**, Colosó, estación de primates, IAvH 5953; San Luis de Onofre (ICN 42299). **Tolima**, Carmen de Apicalá, Río Analí (ICN 11161); Chaparral (ICN 43282-91), Cuira (ICN 22512-14); Ibagué, 7.3 km S Juntas, 1580 m (ICN 9246); Icononzo, Quebrada Las Lajas, 3.5 km E Icononzo, 1200 m (ICN 8311); Mariquita,, IAvH 4743; Entre Melgar y Carmen de Apicalá, Río Sumapaz (ICN 1951-52, 1954); Venadillo, Finca La Estancia, 350 m (ICN 43173).

HYLA PUGNAX(249)

Amazonas, P. N. N. Amacayacu, IAvH 2071; **Antioquia**, La Promesa, Río Nechi, IAvH 2775; corregimiento San Miguel, Hda Soñadora (ICN 36978, 36980); Turbo (1 uncatalogued). **Atlántico**, Piscicultra Soplaviento, IAvH 582, 586; Polonuevo, 1 km SW Polonuevo, Vereda Los Charcos (ICN 44414-15); Puerto Colombia (ICN 1021-23, 31549-50); Km 6 a Puerto Colombia (ICN 26123-29, 31557); Soledad (ICN 226-27). **Arauca**, Arauca, casa de Hato el Venero, IAvH 444, 2503-04, 2982, 3697-3700, 3902, 3905; Caño Limón, Asoc. Cravo Norte, Relleno Sanitario (ICN 27699, 27806-07); Yarumal via Malanegra (ICN 26735); Vivero (ICN 27705). **Bolívar**, Mompos (ICN 26274); Santa Catalina, Hda. El Ceibal (ICN 44416-61); Santa Rosa (ICN 2101, 2109-21, 2248-58, 2267-69, 2271-78, 2290-302); Turbaco, zona Matute, 100 m (ICN 13727-28); Zambrano, Porteria Monterrey (ICN 33222). **Boyacá,** Puerto Boyacá (ICN 35805-06), inspección de policia Puerto Romero (ICNMHN 44667-71, 44712-20), campamento Techin, 320 m (ICNMHN 38054-56), quebrada La Honda (ICNMHN 38065), Vereda La Cristalina, 365-375 m (ICNMHN 38063), Vereda La Fiebre, finca La Barrilera, 340-420 m (ICNMHN 38051-53, 38066-67) quebradas Las Fiebrecilla y Friebrecita, 300 m (ICNMHN 38057-62), Vereda Las Mercedes, finca Los Balcones, 380 m (ICNMHN 38041-50, 38064). **Caldas**, La Victoria, Km 15.6 carr. La Victoria a la central (ICNMHN 34533-38). **César,** La Gloria, ciénaga de Morales, 80 m (ICNMHN 37308, 37310), ciénaga de Simaña (ICNMHN 18843), Hda Montecarlo, 160 m (ICNMHN 37276-80). **Chocó,** P. N. N. Katios (2 uncataloged). **Córdoba**, Montería, estación piscícola, Univ. Córdoba, 20 m (ICNMHN 19552-54); San Andrés de Soplaviento, IAvH 5095-96; Tierra Alta, Quebrada El Gallo, 100 m (ICNMHN 39153), Quebrada. La Mina, 120-135 m (ICNMHN 39154-55), Represa Urrá (08° 01' N, 76° 13' W), 70-150 m (ICNMHN 43399-413), Vereda Cañas Finas, Quebrada El Golero, 130-180 m (ICNMHN 39156), Vereda Tucurá, Quebrada Lavate y Lourdes, 110-130 m (ICNMHN 39157). **Guajira,** Maicao, corregimiento Calabacito, El Cerrejón, 130 m (ICNMHN 11824-25). **Magdalena**, Minca (ICNMHN 3863); Parque Tayrona, IAvH 2059, 2062, 2064, Cañaverales (ICNMHN 33115). **Meta,** Puerto Gaitan, Vereda San Miguel, fundación Yamato (ICNMHN 38283). **Norte de Santander**, Astillero, casco urbano, 260 m (ICNMHN 33551-57). **Santander**, Landázuri, Hda. Las Flores, 450 m (ICNMHN 8796). Vélez, zona Carare, campo Capote (ICNMHN 613-15). **Sucre**, Colosó, proyecto primates, IAvH 1167. Galeras, Vereda La Coracera (ICNMHN 42738). San Luis de Onofre (ICNMHN 42289). San Marcos, estación crocodilia, IAvH 5337, 5703.

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